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THE
BOTANICAL GAZETTE

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REVERSIBLE SEX-MUTANTS IN *LYCHNIS DIOICA*¹

GEORGE HARRISON SHULL

(WITH FIFTEEN FIGURES)

Six hermaphrodite specimens of *Lychnis dioica* L. were found in cultures of 1908, and eight in 1909. With respect to their hereditary behavior in the first generation, when used as pollen parents, these hermaphrodites proved to be of two kinds, the individuals *A* and *B* being capable of determining the hermaphrodite character in their male offspring, while individuals *C* and *D* behaved exactly like normal males, giving progenies consisting of females and normal males.

The conclusion was reached (SHULL 26) that the hermaphrodites are modified males, because (1) in all families in which the first mentioned type of hermaphrodite was used as the pollen parent the offspring consisted of females and hermaphrodites in the same ratio as would have been expected of females and males if a normal male had been used as the pollen parent, and because (2) the second type of hermaphrodite when used as a pollen parent gave the same result that a normal male would have given.

Accepting tentatively the Mendelian explanation of sex first clearly enunciated by CORRENS (6), which recognizes the one sex as homozygous and the other sex as heterozygous with respect to a sex-producing gene, it was decided that these hermaphrodites (and therefore also males) must be heterozygous, because (1) the males are capable of being modified in such manner as to display function-

¹ Read at the meeting of the Botanical Society of America, Minneapolis, December, 1910.

al organs of both sexes, and because (2) self-fertilized hermaphrodites produce dimorphic progenies, consisting of females and hermaphrodites.

In my first paper on the inheritance of sex in *Lychnis* (SHULL 26), I represented the sex genes by the conventional signs for the sexes (♀, ♂, and ♂). As these signs were used in my tables with two different meanings—to represent sometimes the character of the genes and at other times the character of the soma—I suspect that readers may have experienced some difficulty in comprehending the tables. I shall therefore adopt here the plan usually followed by students of genetics, of representing the genes by letters, letting *Ff* be respectively the presence and absence of a female determiner, *Mm* a male determiner, and *Hh* a hermaphrodite determiner. The conventional signs for the sexes will be used in this paper only in their more usual signification, referring to the nature of the soma, that is, the sporophyte.

If CORRENS' view of sex determination is correct, and the males are heterozygous, the females must be homozygous. CASTLE (5) suggests that in such a case the females will always be *positive* homozygotes, having a pair of sex genes (*FF*) corresponding with a single equivalent gene (*Ff*) in the male. I do not believe that this view can be substantiated, as there seems no good reason why females should not be negative homozygotes in some plants and animals, "neutral" homozygotes in others, and positive homozygotes in a third class. If the females are positive homozygotes, the somatic formula of the two sexes may be represented thus: *FF*=♀, and *Ff*=♂; if the females are negative homozygotes, the corresponding symbols will be *FFmm*=♀, and *FFMm*=♂; and if the female is a "neutral" homozygote, the formulae of the two sexes will be *FF*=♀, and *FM*=♂. Only the first two of these assumptions concerning the nature of the females were considered in my earlier paper, and either was found capable of explaining the results secured in the first generation, provided the presence of a partially independent hermaphrodite factor (*H*) might also be assumed.

Whether there was any genetic relationship between the hermaphrodites *A* and *B* which produced hermaphrodite offspring, and *C* and *D* which produced males, could not be determined in the first

generation, and two explanations seemed possible: (1) these two types of hermaphrodites might be respectively homozygous and heterozygous in regard to a modifying factor *H*, whose presence was assumed, on the suggestion of CORRENS, as possibly necessary for the change of a normal male into a hermaphrodite; (2) the hermaphrodites of the second type (*C* and *D*), which gave first generation progenies equivalent to those produced by normal males, might owe their hermaphrodite character to some accident of development which affected the soma alone, leaving the germ cells unchanged. In this case they might be appropriately called "somatic hermaphrodites," to distinguish them from those of the first type (*A* and *B*) which transmitted the hermaphrodite character to their male offspring and which are therefore to be recognized as "genetic hermaphrodites" or true hermaphrodite mutants.

Neither the character of the females nor the relationship of the two types of hermaphrodites could be determined from the results of the first generation, but it was obvious that at least a partial solution could be expected from the second generation. To attain this end a large number of crosses were made in 1909, by using hermaphrodite individuals and their derivatives in various combinations with each other, with unrelated females, and with normal males. The offspring of these crosses were grown during the summer of 1910, and the 104 families produced from them included 6132 individuals which came to bloom and of which the sex was recorded. These records were made in the writer's absence by Mr. R. CATLIN ROSE, to whose energy, faithfulness, and care it gives me pleasure to testify.

In order to comprehend fully the problems involved, it will be advantageous to consider some assumptions which were permitted by the results of the F_1 crosses, and whose availability is partially tested in the F_2 families reported in the present paper. In this connection it is also important to consider briefly the "presence and absence" hypothesis, a full discussion of which, however, would require too great a digression. Although this so-called hypothesis is frequently referred to by students of genetics, I am not aware that it has ever had a very definite formulation, and it would undoubtedly be defined differently by different students.

"Presence and absence" came into use in the first place, simply as a convenient method of expression to avoid the confusion which arises when the same dominant character is described as an alternative of several different characters which are hypostatic to it, and which may themselves be present or absent in any particular instance. The very general applicability of this mode of expression naturally suggested to various writers (HURST 18, SHULL 27, etc.) that it might have a more fundamental significance than merely as a convenient form of description. These authors considered it simpler and more practical to suppose that the heterozygous genes are unpaired, and that the "*absence*" of a character² is unrepresented by any internal unit corresponding with the gene which determines the "*presence*" of that character. The "presence and absence" hypothesis need not be associated, however, with the conception of unpaired determiners in the heterozygote, for in any *pair* of organs there may be present a function or feature in one member of the pair which is absent in the other member, or both members may be alike in kind but different in quantity or activity, the differential between the two being in this case the determiner of the alternative characters involved. This excess in one member of the pair would be present, of course, in that member only, and must be absent in its mate. Whether the hypothesis of unpaired genes or that of paired genes represents the true condition in any particular instance, and whether the absence of a character is absolute or only relative, will not interfere in the least with the use of "presence and absence" as the most convenient method of stating a great majority of the alternative characters with which the student of heredity has to deal. For the application of these different phases of the "presence and absence" hypothesis to the sex problem in *Lychnis*, attention is directed to the following table:

² It is to be regretted that some writers have misconstrued the meaning attached by most geneticists to the expression "absence of a character." The absence of the Angora character in cats, rabbits, etc., does not result in a hairless animal, but one with short hair. In *Oenothera* the absence of *rubricalyx* pigmentation does not prevent the production of anthocyan in the amount and localization characteristic of *O. rubrinervis* (see GATES, R. R., Studies on the variability and heritability of pigmentation in *Oenothera*. Zeitsch. Ind. Abst. Vererb. 4:337-372. 1911).

TABLE I
PRIMARY ASSUMPTION I.—There is a separate factor *H* which changes the male to a hermaphrodite, but which cannot find expression in the female.
SECONDARY ASSUMPTION I.—The two types of hermaphrodite are respectively homozygous and heterozygous in the factor *H*.

WHEN THE FEMALE IS	FORMULAE		REQUIRED ASSUMPTION	HYPOTHETICAL COMBINATIONS	EMPIRICAL RESULTS	REMARKS
	female	hermaphrodite				
Positive, and <i>H</i> homozygous <i>H</i> heterozygous	<i>FFhh</i>	<i>FjHH</i> { <i>H</i> coupled with <i>F</i> } { in heterozygote }	<i>FFHh</i> and <i>FjHh</i> <i>FFHh</i> and <i>Fjhh</i>	♀ and ♂ ♀ and ♂	The correctness of these assumptions would result in: { <i>F</i> ₁ ♀'s with latent <i>H</i> } { <i>F</i> ₁ ♂'s unlike <i>P</i> ₁ ♂'s. }
	<i>FFhh</i>	<i>FjHh</i>				
Negative, and <i>H</i> homozygous <i>H</i> heterozygous	<i>FFmhlh</i>	<i>FFMmHH</i> { <i>H</i> allelomorphic to { } { <i>M</i> in heterozygote }	<i>FFmmHh</i> and <i>FFMmHh</i> <i>FFmmHh</i> and <i>FFMmhlh</i>	♀ and ♂ ♀ and ♂	
	<i>FFmhlh</i>	<i>FFMmHh</i>				
Neutral, and <i>H</i> homozygous <i>H</i> heterozygous	<i>FFhh</i>	<i>FMHH</i> { <i>H</i> coupled with <i>F</i> } { in heterozygote }	<i>FFHh</i> and <i>FMHh</i> <i>FFHh</i> and <i>FMhlh</i>	♀ and ♂ ♀ and ♂	
	<i>FFhh</i>	<i>FMHh</i>				

TABLE I—Continued

SECONDARY ASSUMPTION II.—The second type of hermaphrodite is purely somatic and unrelated to the first type, and the first type is then heterozygous in respect to H .*

WHEN THE FEMALE IS	FORMULAE		REQUIRED ASSUMPTION	HYPOTHETICAL COMBINATIONS	EMPIRICAL RESULTS	REMARKS
	female	hermaphrodite				
Positive, and Genes unpaired Genes paired ... Negative..... Neutral.....	$FFhh$ $FFhh$ $FFmhh$ $FFhh$	FHh Ffh $FFMhHh$ $FMHh$	H allelomorphic to F H coupled with f H coupled with M H coupled with M	$\{ FFhh \text{ and } FfHh$ $FFmhh \text{ and } FFMhHh$ $FFhh \text{ and } FMHh$	$\{ \begin{matrix} \text{♀ and } \text{♂} \\ \text{♀ and } \text{♂} \\ \text{♀ and } \text{♂} \end{matrix}$	$\{ \begin{matrix} \text{♂'s cannot transmit} \\ \text{hermaphroditism,} \\ F_1\text{♂'s are like } P_1\text{♂'s} \end{matrix}$

PRIMARY ASSUMPTION II.—There is no factor H , hermaphroditism being caused by a mutative modification of the sex gene, which may then be represented by M_H , F_H , or f_H .

Positive, and Genes unpaired Genes paired ... Negative..... Neutral.....	FF FF $FFmm$ FF	F_Hf Ff_H FFM_H^m FM_H $\left. \begin{matrix} \text{Chance distribution} \end{matrix} \right\}$	$\{ \begin{matrix} \text{None that could result} \\ \text{in } \dots \\ FF \text{ and } Ff_H \\ FFmm \text{ and } FFM_H^m \\ FF \text{ and } FM_H \end{matrix} \}$	$\{ \begin{matrix} \text{♀ and } \text{♂} \\ \text{♀ and } \text{♂} \\ \text{♀ and } \text{♂} \\ \text{♀ and } \text{♂} \end{matrix}$	$\{ \begin{matrix} \text{The } \text{♀} \text{ cannot be positive} \\ \text{unless } F \text{ has a synaptic} \\ \text{mate} \\ \text{♂'s cannot transmit her-} \\ \text{maphroditism} \\ F_1 \text{ } \text{♂'s same as } P_1 \text{ } \text{♂'s} \end{matrix}$
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* The case in which H is homozygous in the genetic hermaphrodites has been already tabulated under secondary assumption I.

Particular attention should be given to only two points in this table until after the results secured in the second generation have been considered. The assumptions which form the basis of the first section of the table lead to the expectation (*a*) that females derived from hermaphrodite families, whether they be fertilized by normal males or by their hermaphrodite sibs, will yield families in which the male offspring are hermaphrodite and normal male in equal numbers; and (*b*) that the hermaphrodites of the second generation when used to fertilize females from normal male families will produce no hermaphrodites, but only females and males. The alternative assumptions involved in the second and third sections of the table, on the other hand, lead to the expectation that, regardless of the origin of the female, no hermaphrodites will be produced normally, except when fertilization is brought about by sperms from a genetic hermaphrodite, and then the result will always be the same whether this hermaphrodite was a mutant or whether it was derived from an antecedent hermaphrodite.

We may now proceed to examine the results of the crosses. This will be most easily accomplished by considering each type of cross separately in the following fourteen cases. In the model pedigrees, illustrated under each case, the oldest ancestors entered in the diagrams are females and males both of which came from normal families, whose matings had been controlled during at least three still earlier generations, and which are known to have been in each such previous generation the result of crosses between females and normal males, and to have belonged to families in which no hermaphrodite mutants appeared. In the diagrams all male and hermaphrodite individuals which appeared as mutants are indicated as such, and it should be understood that any male or hermaphrodite not so marked was a member of a family which consisted of a normal proportion of its own type, that is, either male or hermaphrodite.

CASE I

CROSSES OF GENETIC HERMAPHRODITE MUTANTS WITH FEMALES

Only 2 of the 8 plants recorded as hermaphrodites in 1909, in otherwise normal male families, were successfully used for breeding. One of these, bred to 2 different unrelated females, produced 72

females and 88 hermaphrodites (nos. 09123 and 09171). The other, bred to the same 2 females, produced 116 females and 53 hermaphrodites (nos. 09124 and 09172). The result of these four crosses, involving 2 hermaphrodite mutants, was therefore 188 females and 141 hermaphrodites, thus showing that these 2 hermaphrodite mutants were of the same character as the two denomi-

Pedigree no.	Result	Pedigree no.	Result
0869	58♀:36♀:1♂	08150.....	59♀:43♀
08106.....	53♀:50♀	09123.....	36♀:53♀
08118.....	60♀:40♀:1♂	09124.....	52♀:30♀
08127.....	51♀:52♀	09171.....	36♀:35♀
08128.....	50♀:51♀	09172.....	64♀:23♀
08149.....	67♀:33♀	Total.....	586♀:446♀:2♂

nated *A* and *B* in my earlier report. For the sake of completeness, the crosses of *A* and *B* already reported are included in the tabulation of these crosses, the total progeny from this type of cross being 586 females, 446 hermaphrodites, and 2 males.

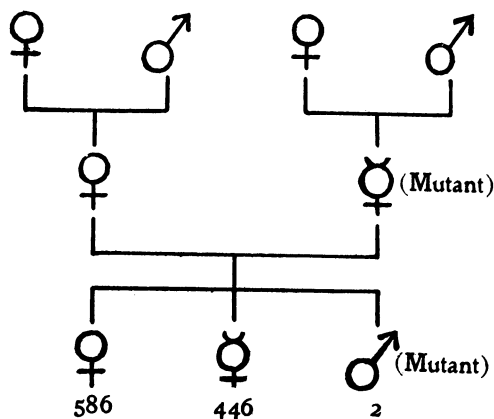


FIG. 1.—Model pedigree for case I

Two other individuals, which had a derangement of the sexual characters of such a nature that the lobes of the calyx were transformed into stigmas, and in one instance a small ovary with apparently functional stigmas was present in the center of the flower and

associated with functional stamens, were of such anomalous character that they have not been included among the 8 recognized hermaphrodites found in normal families in 1909, but they will be mentioned later under case XIII in connection with the somatic hermaphrodites *C* and *D* of my preliminary report.

CASE II

WHEN GENETIC HERMAPHRODITE MUTANTS ARE SELF-FERTILIZED

Pedigree no.	Result
08115.....	24♀: 19♂
08117.....	9♀: 6♂
08119.....	110♀: 95♂
Total.....	143♀: 120♂

None of the new hermaphrodite mutants discovered in 1909 were successfully self-fertilized, and the pedigrees here reported are repeated from my former paper for the sake of completeness. All the self-fertilized hermaphrodites which yielded progenies in my 1910 cultures belonged to a later generation, being offspring of a self-fertilized hermaphrodite and not the progeny of new mutants. They consequently belong to a separate case and will be considered next. The agreement of these results with those under case I leads to the conclusion that the eggs of the hermaphrodite are all of one type, that is, female-bearing, like those of the females. The significance of this result will be considered later.

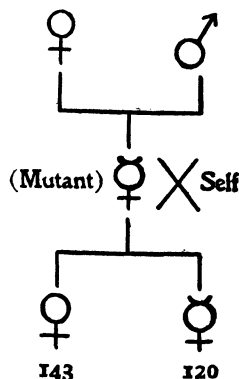


FIG. 2.—Model pedigree for case II.

CASE III

WHEN F_1 HERMAPHRODITES ARE SELF-FERTILIZED

Pedigree no.	Result	Pedigree no.	Result
09185.....	5♀: 8♂	09217.....	16♀: 9♂
09186.....	17♀: 6♂	09218.....	17♀: 1♂
09187.....	18♀: 23♂	09219.....	22♀: 5♂
09191.....	6♀: 10♂: 1♂	09220.....	2♀: 2♂
09216.....	1♀	09222.....	43♀: 38♂: 1♂
		Total.....	147♀: 101♂: 3♂

The first four of these families were produced by self-fertilizing 4 individuals of pedigree number 08115, and the rest by self-fertilizing 6 individuals of number 08119. Most of these families were too small to show obvious differences in the genetic composition of the different parent plants, or between them and the

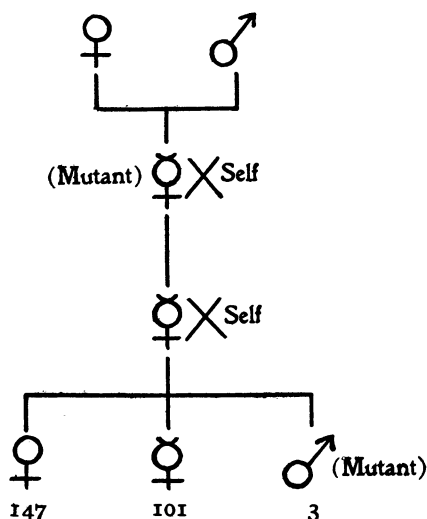


FIG. 3.—Model pedigree for case III

hermaphrodite mutants tested under case II. The small size of the families is due to the comparatively poor development of the ovaries and stigmas in most hermaphrodites, and the consequent difficulty of securing large quantities of seeds by self-fertilization. Most of the attempts to self-fertilize the hermaphrodites resulted in failure, and only in a small proportion were any seeds produced. The total result agrees with results secured from the observation of larger families, and it is fair to assume that the relatively

large differences shown by some of these families are not significant because of the smallness of the progenies. This conclusion will be fully justified I believe, when it is observed under case IV that the very same plants, which produced the somewhat variable progenies shown above, gave uniform results when they were crossed with an unrelated female.

CASE IV

WHEN HERMAPHRODITES FROM THE PROGENY OF A SELF-FERTILIZED HERMAPHRODITE MUTANT ARE CROSSED WITH AN UNRELATED FEMALE

The families 09133 to 09142, inclusive, resulted from pollinating different flowers of a single female, 08114(4), with the pollen from 10 different hermaphrodites taken consecutively in family 08115, and the remaining 19 families were produced by pollinating the same female, 08114(4), with pollen from 19 different hermaphrodites

in family 08119. This series of experiments, like those under case III, was calculated to discover any genetic differences which

Pedigree no.	Result	Pedigree no.	Result
09133.....	44♀:20♂:1♂	09154.....	57♀:26♂
09134.....	55♀:27♀	09155.....	48♀:42♀
09135.....	41♀:37♀	09156.....	54♀:41♂
09136.....	42♀:31♂	09157.....	56♀:32♀
09137.....	47♀:33♀	09158.....	59♀:25♀
09138.....	47♀:37♀	09159.....	51♀:29♀
09139.....	50♀:29♀	09160.....	43♀:29♀
09140.....	65♀:25♀	09161.....	52♀:29♀
09141.....	38♀:34♀	09162.....	25♀:30♀
09142.....	51♀:40♀	09163.....	56♀:33♀
09149.....	52♀:25♀:1♂	09164.....	16♀:14♀
09150.....	49♀:30♀	09165.....	46♀:40♀
09151.....	51♀:45♀	09166.....	36♀:19♀
09152.....	66♀:24♀:1♂	09167.....	36♀:19♀
09153.....	49♀:22♀		
		Total.....	1382♀:867♂:3♂

might exist among F_2 hermaphrodites, and the fact that these 29 different individuals when crossed with a single female produced

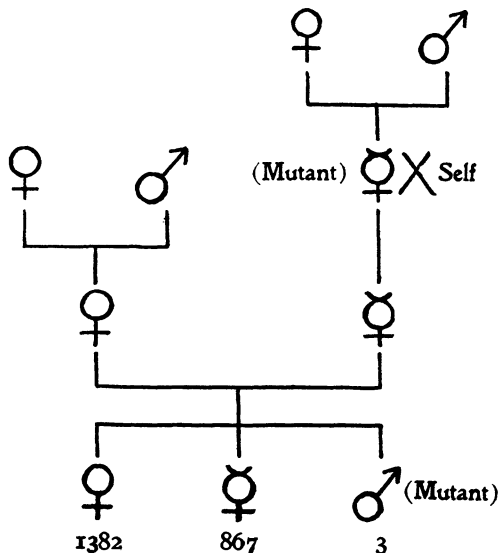


FIG. 4.—Model pedigree for case IV

essentially identical results leads to the conclusion that no such genetic differences existed. This conclusion is apparently open to

but one criticism; the characters of the female chosen to be the mother of all these families might dominate such different characters as were possessed by the hermaphrodites, in which case all families would show identical composition regardless of the variations in the pollen parents. This suggested dominating influence of the female is rendered untenable, however, by the fact that the same female was pollinated by 7 other hermaphrodites having different histories from those considered under the present case, and also by 11 different males of diverse origin, and in every case the males among the progenies were of the same type as their pollen parent.

CASE V

WHEN FEMALE OFFSPRING OF SELF-FERTILIZED HERMAPHRODITES ARE CROSSED WITH AN UNRELATED MALE

Pedigree no.	Result	Pedigree no.	Result
09174.....	21♀: 8♂	09190.....	49♀: 22♂
09170.....	50♀: 34♂	09193.....	28♀: 25♂: 1♀
09178.....	34♀: 20♂: 1♀	09196.....	33♀: 23♂
09180.....	39♀: 11♂	09198.....	58♀: 34♂
09182.....	36♀: 17♂	09200.....	26♀: 22♂
09184.....	42♀: 34♂: 2♀	09202.....	22♀: 17♂
09189.....	12♀: 6♂	09204.....	21♀: 32♂
		Total.....	471♀: 305♂: 4♀

These families were produced by pollinating 14 different females, taken consecutively in 08115, with pollen from a single normal male, 0855(36), in an unrelated family. The essentially equal results of all these crosses indicate that there are no differences among these females which were not dominated by the sex character of the pollen parent. As this pollen parent was a male from a normal male parentage, it may be appropriately assumed to have been free from any hypothetically possible hermaphrodite modifier *H*. If such a modifier had been possessed by any of these 14 females, a more striking evidence of that fact should be presented than is found in the occurrence of less than 1 per cent of hermaphrodite individuals among the offspring. This is a smaller percentage of hermaphrodites than has been found in one or two cases among the offspring of a female pollinated by a normal male, neither

parent having had any hermaphrodite connections. It appears fair, therefore, to consider these four hermaphrodites simply as mutants, and not as genetic derivatives from their maternal grandfather. The few hermaphrodites occurring in the families included under the present case may be related to the fact, however, that the females belong to a hermaphrodite family, for the same male 0855(36) was crossed with seven other females and with one hermaphrodite, and among the 443 offspring produced there were no other hermaphrodites.

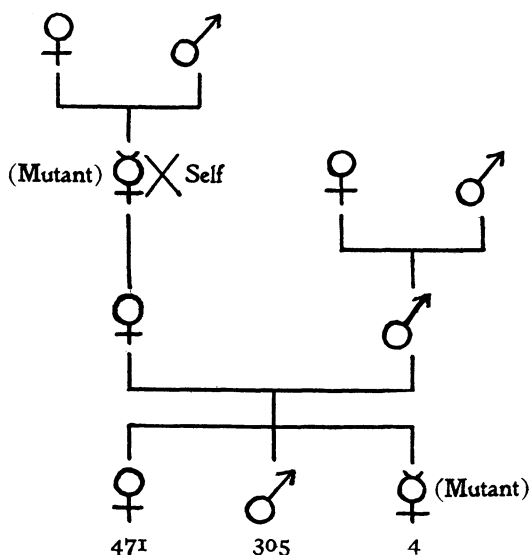


FIG. 5.—Model pedigree for case V

Allowing for the same frequency of occurrence of hermaphrodites as shown in the table above, there should have appeared among these 443 individuals derived from the same male crossed with other females at least two hermaphrodite mutants. This number is so small that they may possibly have been omitted through the errors of random sampling, but the suggestion may be made that while a female cannot transmit hermaphroditism to its offspring, it may perhaps supply an intracellular environment favorable to the mutation of the male genes into hermaphrodite genes.

CASE VI

WHEN THE DAUGHTERS OF A SELF-FERTILIZED HERMAPHRODITE ARE CROSSED WITH ONE OF THEIR HERMAPHRODITE SIBS

Pedigree no.	Result	Pedigree no.	Result
09173.....	6♀: 2♂	09192.....	9♀: 2♂
09175.....	23♀: 13♂	09195.....	39♀: 17♂
09177.....	32♀: 17♂	09197.....	48♀: 6♂
09179.....	45♀: 28♂	09199.....	40♀: 20♂
09181.....	63♀: 16♂	09201.....	40♀: 7♂
09183.....	4♀: 3♂	09203.....	35♀: 10♂
09188.....	36♀: 7♂	09205.....	9♀: 7♂
		Total.....	429♀: 155♂

The seed parents of these families were the same 14 females which produced the families considered under case V. In the present case they were all pollinated by a single hermaphrodite, 08115(9), in the family to which they themselves belonged. The results correspond closely with those of the last section, except that in this case the males were invariably hermaphrodites, showing as before that the character of the pollen parent determines the sex character of the male offspring. It may be noted that most of these families contained a strikingly high percentage of females, as compared with those under case V, there being 73.46 per cent of females among the progenies of case VI, and only 60.7 per cent among those of case V.

The meaning of such differences in the sex ratios is quite unknown at the present time, and no discussion of the series of experiments which are in progress for the purpose of finding an interpretation of such variable ratios will be undertaken here. It is believed, however, that the question of the sex-ratios constitutes an altogether different problem, and has no direct bearing upon matters relative to the genetic interrelationships of the different sexual types, which are alone under consideration in this paper.

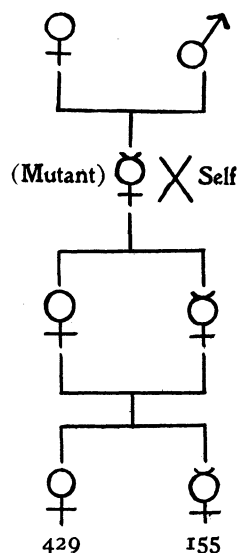


FIG. 6.—Model pedigree for case VI.

CASE VII

WHEN HERMAPHRODITE OFFSPRING OF AN OUT-CROSSED HERMAPHRODITE MUTANT
ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result	Pedigree no.	Result
09112.....	36♀:18♂:1♂	09118.....	46♀:42♂
09113.....	56♀:31♂	09145.....	46♀:49♂
09114.....	7♀: 3♂	09146.....	50♀:39♂
09115.....	20♀:14♂	09148.....	55♀:24♂
09116.....	39♀:26♂	09260.....	26♀:27♂
09117.....	47♀:19♂	Total.....	428♀:292♂:1♂

These families are essentially similar in nature to those considered under case IV, except that in the present case the mutant was crossed with an unrelated female instead of being self-fertilized. The first 7 of these families were produced by crossing 7 different

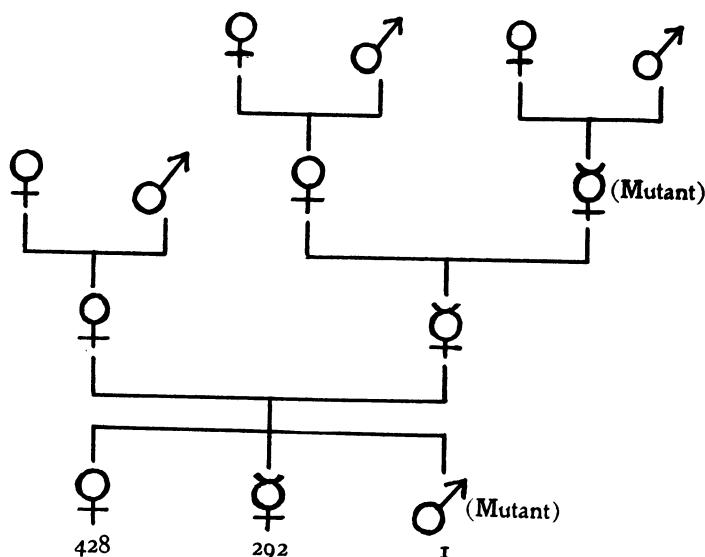


FIG. 7.—Model pedigree for case VII

hermaphrodites in 08118, upon a single female, 08109(1); the next three (09145-09148) were the result of using three of the same hermaphrodite individuals in the pollination of the female, 08114(4), which was used as the seed parent of all the families included under

case IV. The genetic equivalence of the different hermaphrodites again stands out clearly in these results, and when the ratios of the two series are compared, it is found that the percentage of hermaphrodites produced by the hermaphrodite offspring of a self-fertilized hermaphrodite is slightly lower than that produced by the offspring of these cross-bred hermaphrodites, the former producing only 38.2 per cent of hermaphrodites and the latter 42.6 per cent. The difference is too small to be of significance, particularly in view of the fact that much wider differences than this are found in families produced from different seed capsules on a single plant when pollinated by a single male. It might have been expected, perhaps, that a self-fertilized hermaphrodite would have produced a larger percentage of hermaphrodites than would be produced by the same hermaphrodite crossed upon a female of a normal family. The fact that such a result does not appear is further proof that, although the hermaphrodite is a heterozygote, its egg cells are of a single type and like those of the normal females.

The last family under this section was produced by crossing a hermaphrodite of 08128(16) upon a female in a genotypically distinct strain of *Lychnis dioica*, received several years ago from the vicinity of Harrisburg, Pennsylvania. The result is quite the same as in the other families, all of which were derived from a common stock secured at Cold Spring Harbor, Long Island.

CASE VIII

WHEN HERMAPHRODITES ARE POLLINATED BY NORMAL MALES

Pedigree no.	Result
08116	21♀:11♂:2♂
09215	8♀: 1♂
Total.....	29♀:12♂:2♂

I have already remarked the difficulties encountered in the use of hermaphrodites as self-fertilized seed parents. The difficulties are still greater when the problem requires the crossing of the hermaphrodites with other males, for nearly all the numerous castrations which have been made have resulted in the dropping

of the flowers without further development. Only one family (08116) was produced in 1909 from a cross of this kind. It was

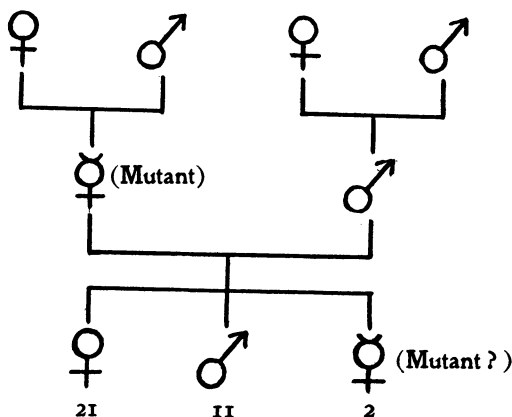


FIG. 8.—First model pedigree for case VIII

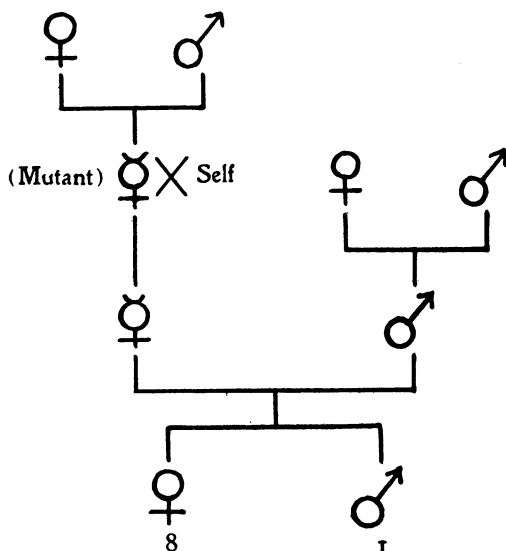


FIG. 9.—Second model pedigree for case VIII

reported upon in my preliminary paper, and is repeated here. The occurrence of two hermaphrodites in this small family suggested that the hermaphrodite character might be inherited from the

mother as well as the father. On this account the cross between hermaphrodites and males must be considered the most important of all combinations in interpreting the relations of the sexes. The difficulty involved in the castration of the flowers permits the question whether the two hermaphrodites may not have been due to a faulty technique, for males produced from unintentional self-pollinations would be hermaphrodites.³ Special efforts were put forth in 1909 to secure more crosses of this character, but these resulted in a single success, and that of so limited extent as to be wholly indecisive. The 9 offspring of this cross (09215) consisted of 8 females and 1 male, so that the little evidence which such a small family can give is in harmony with the proposition that the character of the female parent has no influence upon the sex characters of the male offspring, except possibly by supplying an intracellular environment which is favorable or unfavorable to the occurrence of sex mutation, suggested under case V. Continued efforts are being made to secure more data from combinations of hermaphrodites with normal males.

CASE IX

WHEN HERMAPHRODITE OFFSPRING OF A HERMAPHRODITE MOTHER AND NORMAL MALE FATHER ARE CROSSED UPON AN UNRELATED FEMALE

Pedigree no.	Result
09143	38♀:38♂
09144	51♀:33♂
Total.....	89♀:71♂

The appearance of 2 hermaphrodites in family 08116 of case VIII immediately raised the question whether they were true genetic hermaphrodites like *A* and *B*, or whether they might not be somatic hermaphrodites whose hermaphrodite character was not in any way related to the fact that they were the offspring of a hermaphrodite seed parent. If they should prove to be somatic

³ In a family grown in 1911 from a cross between a white-flowered hermaphrodite and a homozygous blue-flowered male, all the offspring were blue-flowered and several (less than 6 per cent) were hermaphrodite, thus showing that such hermaphrodites are not in this instance due to any unintentional self-fertilization.

hermaphrodites, they would be in reality of the same genotype as their pollen parent, thus offering no exception to the general rule that the male parent determines the sexual type of its male offspring.

Both of these hermaphrodites were crossed upon female 08114(4), already mentioned in cases IV and VII. No influence of the male grandparent appears, as all of the male offspring in these two

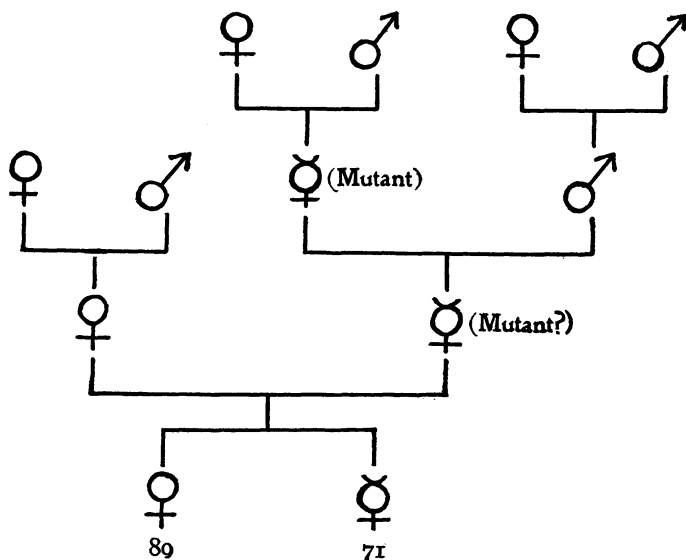


FIG. 10.—Model pedigree for case IX

families were hermaphrodites. This result proves that the 2 hermaphrodites of 08116 were genetic hermaphrodites. One of these hermaphrodites was also self-fertilized and gave a progeny of a single hermaphrodite, constituting family number 09210. It would be rash to draw a conclusion from a family consisting of a single individual, and nothing could have been derived from it if by chance that individual had been a female. The fact that it was hermaphrodite instead of normal male, however, confirms the conclusion that the hermaphrodite parent was a genetic hermaphrodite like its own seed parent.

Whether these two hermaphrodites owed their hermaphrodite character directly to their hermaphrodite mother, or whether it

resulted from a mutation of the male genes received from their father, cannot be definitely decided, but further experiments are in progress to test the possibility that the eggs of hermaphrodites can carry hermaphroditism and may therefore sometimes transmit it to their offspring. The evidence thus far is against their doing so to any considerable extent.

CASE X

CROSSES BETWEEN FEMALES AND THEIR HERMAPHRODITE SIBS IN A FAMILY PRODUCED BY CROSSING HERMAPHRODITE AND MALE

Pedigree no.	Result
09207	1♀: 1♂
09208	12♀: 9♂: 1♂
09209	46♀: 30♂: 1♂
09211	36♀: 17♂
09212	32♀: 16♂
Total	127♀: 73♂: 2♂

These are crosses in which the same 2 hermaphrodites of 08116, discussed in case IX, were used as the pollen parents in crosses with

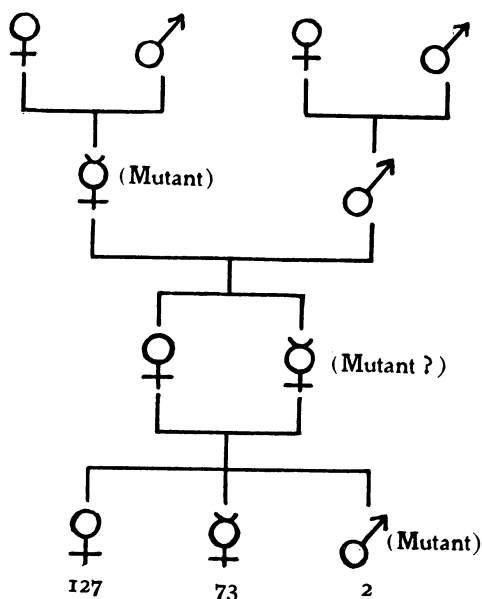


FIG. 11.—Model pedigree for case X

three different females in the same family. The results may be compared with those under case VI, where sib crosses were also dealt with. The comparison shows that the results were identical, though in one case the parents were the progeny of a self-fertilized hermaphrodite, while in the other the parents resulted from the cross of a hermaphrodite fertilized by a male. Thus is given still further evidence that these hermaphrodites in 08116 were genetic hermaphrodites and that such hermaphrodites are of like hereditary capacity, whatever their origin.

CASE XI

WHEN DAUGHTERS OF A HERMAPHRODITE MOTHER AND MALE FATHER ARE CROSSED WITH AN UNRELATED MALE

Pedigree no.	Result
09206.....	7♀: 5♂
09213.....	10♀: 8♂
09214.....	33♀: 21♂
Total.....	50♀: 34♂

The first of these families (09206) had the same seed parent as the first two families (09207 and 09208) under case X, and the

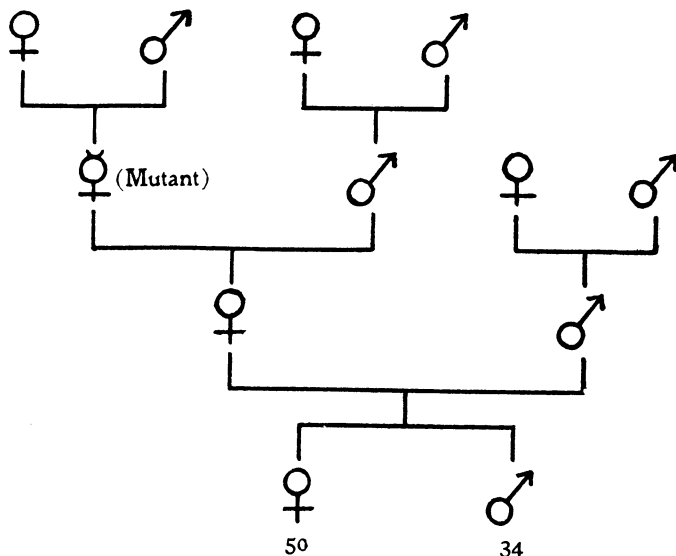


FIG. 12.—Model pedigree for case XI

second (09213) had the same seed parent as the last two families (09211 and 09212) under that case. The pollen parent in all three families of the present case was the same normal male, 0855(36), that was used for all the crosses in case V. It is consequently fair to assume that the differences in the result under case X and case XI are wholly referable to the male parent, and that such differences as appear between case X and case V are referable to the seed parents. There is no difference in the latter instance, while the fundamental difference in the former is that in case X the males were hermaphrodite, while in the present case they were normal males, thus showing again the correspondence between the male offspring and their pollen parent.

CASE XII

WHEN MALE MUTANTS ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result
09147.....	40♀:40♂
09239.....	43♀:44♂
Total.....	83♀:84♂

It will be recalled that among the 705 offspring produced in 1909 from crosses between females and the genetic hermaphrodites, *A* and *B*, there were 2 males and 305 hermaphrodites. In similar manner it will have been noted that in a number of the cultures of 1910 a very small percentage of such males have appeared in families of which the male offspring were generally hermaphrodite. Instances of this kind are noted above, under cases I, III, IV, V, VII, and X. Whether these males were true males or possibly somatically modified hermaphrodites may now be considered.

The families reported under the present case were produced by pollinating two different unrelated females with pollen of 08118(13), one of the two males derived from genetic hermaphrodite fathers in 1909. No hermaphrodites were produced, thus showing that the pollen parent was a true male, and not a hermaphrodite which had suffered the suppression of the female organs because of some purely somatic influence. The frequency of occurrence of such male mutants may be inferred from the fact

that 11 of them appeared among progenies comprising a total of 3331 females and 2126 hermaphrodites. In other words, they constitute about 0.2 per cent of the total progeny of the genetic hermaphrodites when the latter are used as pollen parents. In no single family did more than one such male mutant occur. While these numbers are too small to allow an accurate estimate of the

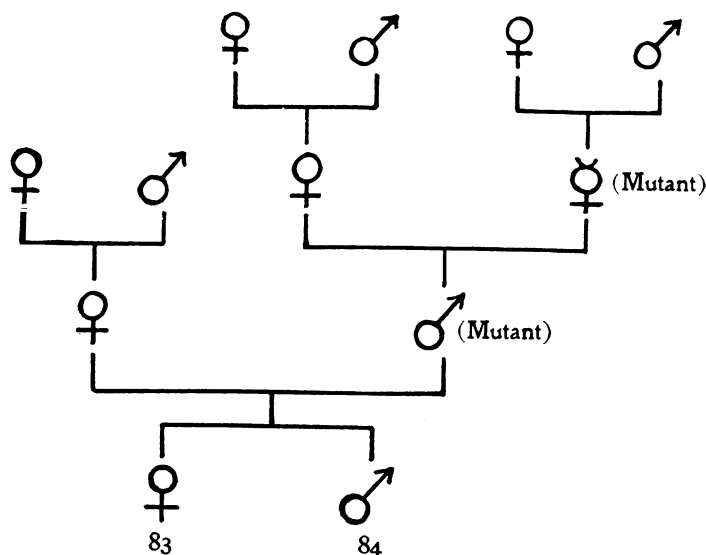


FIG. 13.—Model pedigree for case XII

relative frequency of hermaphrodite and male mutants, the evidence seems to indicate that there is no striking difference between the capacity of males to give rise to hermaphrodite mutants, and that of hermaphrodites to give rise to male mutants, though male mutants have appeared with slightly greater frequency than hermaphrodite mutants.

CASE XIII

WHEN SOMATIC HERMAPHRODITES ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result
08125.....	39♀:55♂
08132.....	26♀:18♂
0995.....	56♀:26♂
0996.....	63♀:34♂
Total.....	184♀:133♂

The pedigrees 08125 and 08132 are those of hermaphrodites *C* and *D* among the cultures of 1909, which were reported upon last year. If the "model pedigree" illustrated in the diagram (fig. 14) be compared with that under case I (fig. 1), the two will be seen to correspond perfectly. In fact, the hermaphrodites *A* and *B* included under case I were full sibs of hermaphrodites *C* and *D* whose progenies are repeated here. These 4 hermaphrodites which were found in the cultures of 1908 were indistinguishable

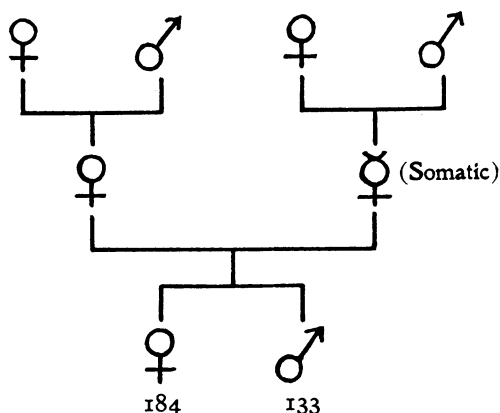


FIG. 14.—Model pedigree for case XIII

from one another in their external characters, and the fact that they belonged in two different categories was only demonstrated by the breeding tests.

No additional instances have been found in which a hermaphrodite indistinguishable from the usual type of "genetic hermaphrodites" has proved to be simply a somatic variation of the male. However, 2 peculiar variant individuals found in one family of the 1909 cultures exhibited an analogous behavior, and consequently their progenies have been added to those of *C* and *D* under this case. The 2 individuals used as pollen parents of the families 0995 and 0996 had several lobes of the calyx prolonged and modified to the form and structure of stigmas, and one of the flowers had in the center a small unicarpellary ovary with an apparently functional stigma. Both of these plants had func-

tional stamens, and both approached more nearly to the type of normal males as the season advanced. On account of the anomalous position of the stigmas in these plants, they are not to be included in the same class with the other hermaphrodites which have been considered, but it may not be unfair to accept the appearance of stigmatic calyx teeth in these male plants as additional evidence that the male is heterozygous in regard to sex, but normally has the presence of the female character completely hidden by the dominance of the male character. A somatic derangement may be assumed as the proximate cause of the appearance of the misplaced stigmas.

These 2 abnormal plants were crossed upon a female sib, 08109(1), and produced together 119 females and 60 normal males, not one of which showed any development of stigmatic calyx lobes or other female characteristics. The female 08109(1) was the one used in case VII for a number of crosses with genetic hermaphrodites, and it was also used as the seed parent in 20 crosses with males of various origin. In all of the other crosses upon this female, the males among the progenies were of the same type as the male parent used in the particular cross from which they sprang, thus showing that this female exerted no modifying influence upon the sex character of her male offspring. This makes it reasonable to conclude that the stigmatic calyx lobes were a purely somatic variation.

CASE XIV

THE SECOND GENERATION FROM A SOMATIC MALE

Pedigree no.	Result
09119.....	50♀:27♂
09120.....	37♀:16♂
09121.....	33♀:26♂
09122.....	61♀:14♂
09168.....	49♀:42♂
09169.....	45♀:10♂
09170.....	58♀:33♂
Total.....	333♀:168♂

In order to make sure that the conclusions drawn from the first generation regarding the character of the hermaphrodites *C* and *D*,

included under cases I–XII produced male offspring like themselves when they were used as male parents (but not when used as female parents). These have been called “genetic hermaphrodites,” to distinguish them from occasional genetic males which possess female organs as a purely somatic modification, and which I have therefore called “somatic hermaphrodites.” These “somatic hermaphrodites” will be omitted from the discussion for the present.

Under cases II and III it is shown that genetic hermaphrodites, of whatever origin, when self-fertilized, yield dimorphic progenies consisting of females and hermaphrodites, thus confirming the conclusions derived from the F_1 . This fact, together with the apparent relative ease with which males are made to exhibit the organs of both sexes, has been accepted as conclusive evidence that the hermaphrodites (and therefore also the males) are heterozygous with respect to sex, and the females homozygous (SHULL 26). In this regard *Lychnis dioica* L. agrees with *Bryonia dioica* (CORRENS 6); with many species of Coleoptera, Orthoptera, Hemiptera, Diptera, Odonata, and perhaps also with Myriapoda and Arachnida (McCLUNG 19, WILSON 38–42, MORGAN 20, 21, STEVENS 31–34, etc.); and with the nematode worms, *Heterakis* (BOVERI 4) and *Ascaris megalocephala* (BORING 3). In man, GUYER (16) has demonstrated that there are two types of sperms, and while the relation of one or other of these types to the type of the egg is unknown, there can hardly be a doubt that here also the female is homozygous and the male heterozygous.⁴

Although these widely divergent groups of plants and animals agree in having homozygous females and heterozygous males, there may still be fundamental differences in the different groups, since there may be three different kinds of homozygotes, and correspondingly different kinds of heterozygotes. This question

⁴ Heterozygous females have now been recognized in *Abraxas* (DONCASTER and RAYNOR 10, and DONCASTER 8, 9), sea urchins (BALTZER 1), canaries (DURHAM and MARRYAT 11), and in domestic fowl (BATESON 2, SPILLMAN 28, 29, GOODALE 12, 13, HAGEDOORN 17, PEARL and SURFACE 24, 25, STURTEVANT 37). GUYER (14, 15) reports two types of sperms in both the guinea fowl and the common fowl, but these observations are out of harmony with all the genetic studies in which sex-limited characters of the Gallinaceae have been involved. The considerable difficulties encountered in the cytological studies on these species suggest the advisability of a repetition of this work.

will be discussed later in connection with the nature of the hermaphrodites.

CORRENS (6, p. 17), with undoubted justification, maintained that the germ cells of monoecious, hermaphrodite, and dioecious species possess the tendency to develop into individuals having the distribution of sex organs characteristic of the particular genotype to which they belong; but when he likens the association of organs of both sexes in the same individual to the mosaic of red and white colors in striped flowers, and of pigmented and white spots in the coats of spotted animals, his justification becomes less obvious. Both striped flowers and spotted pelages are known from many investigations to be due to the presence or absence of a definite Mendelian gene, a so-called "spotting factor" or "pattern factor."

One of the chief aims in the arrangement of my cultures for 1910 was to test the possible existence of such a mosaic or "pattern factor," *H*, as a proximate cause of hermaphroditism in *Lychnis*, and the most striking result secured is the decisive manner in which such a possibility is denied. The hermaphrodite character is not only incapable of reaching expression in the female⁵ (as might be expected, since the female is homozygous), but it is also as a rule not transmitted through the egg cell to the male offspring. The males in the progeny of any cross agree in their sexual type with the male parent of that cross, regardless of its antedecent history. All the assumptions and implications involved in the first section of table I, in which an independent gene *H* was postulated, may therefore be rejected.

⁵I refer here only to the normal functional hermaphroditism with which this paper deals, and not the pseudo-hermaphroditism which results when females of *Lychnis dioica* are attacked by the smut, *Ustilago violacea*, as reported by STRASBURGER (35). I was inclined (SHULL 26) to consider STRASBURGER's interpretation of the effect of *Ustilago* a mistake, as it appeared to me more probable that the infected plants were males whose heterozygous nature easily permitted the development of the female characters. STRASBURGER (36) has shown conclusively, however, by two series of facts, that his original observations and interpretation were correct. These facts are (a) that diseased plants are not always completely infected, in which case the uninfected branches of the pseudo-hermaphrodites have normal female flowers; and (b) that male plants may be infected also, but such infection does not in this case result in the development of the female organs.

In the second section of table I the hypothetical gene H for hermaphroditism is given limitations which make it fit all the empirical results of both the first and subsequent generations; but when the significance of the limitations is taken into account, it becomes evident that there is small advantage gained by the postulation of such a gene. Indeed the only advantage lies in the fact that in case the female is a positive homozygote, it keeps open the question whether or not there is a synaptic mate of F in the normal male; for a newly arisen hermaphrodite gene (H) might conceivably become a synaptic mate of F , even though the latter had had no synaptic mate in the normal male.

If the female is a neutral homozygote, that is, if the female gene F has a male gene M as its synaptic mate in the male, the hermaphrodite gene (if it exist at all) must be absolutely coupled with this male gene. In like manner, if the female is a negative homozygote $FFmm$, the H (if present) must be coupled with the male gene M . It is simpler, however, to assume that the hermaphrodite determiner is a modified form of the sex gene itself, than to suppose that it is a separate gene invariably coupled with the sex gene. This conception that hermaphroditism results from a mutative change in the sex gene, or in its homologue (?), the “Y-element,” is made the basis of the last section of table I, but can apply only to those cases in which a male gene is present, or if not a male gene, then its homologue, a sexually indifferent gene which takes the place of M in the male; for if the hermaphrodite character is assumed to be due to a change in the female gene (F), as it must be if the latter has no “synaptic mate,” the scheme will not work.

It appears to me impossible at the present time to determine whether the females of *Lychnis* are positive, neutral, or negative homozygotes. The facts seem to be equally well met by any of these assumptions; but the definite limitations of the hermaphrodite character to the males makes inapplicable the extreme form of the “presence and absence” hypothesis (that is, the hypothesis of unpaired genes) unless the female is a negative homozygote with reference to a male sex gene (M). While the possibility must be kept open that this is the relationship of the sexes in *Lychnis*,

it seems to me more probable that the female is a neutral homozygote (FF), the male having the formula FM , and the hermaphrodite the formula FM_H . The gradually increasing number of known instances of "spurious allelomorphism" proves that the pairing of unlike or unequal genes in the heterozygote is, if not the general condition, at least a not uncommon one.

The question whether the sex genes are paired or unpaired in the heterozygote, and if unpaired, whether the female is a positive or a negative homozygote, might be settled by simple observation, if it could be known that the chromosomes are the sex determiners, as a number of recent cytological studies clearly suggest. It is not at all certain, however, whether the unequal chromosome groups in the male-producing and female-producing germ cells are active *determiners* or simply passive *indicators* of other more fundamental differences. The latter possibility is strongly emphasized by MORGAN (20), who shows that the pole to which the accessory chromosome in *Phylloxera* is to proceed, is already determined before that chromosome has given any indication, by its own motion, to which pole it will go. This suggests that the poles of the dividing spermatocyte may be sexually differentiated in advance by some other factor. If the chromosomes are not the sex-determiners, but only passive indicators, the fact that they are paired or unpaired, equal or unequal, has no decisive bearing upon the question whether the female is a positive, neutral, or negative homozygote, or whether the genes are paired or unpaired in the heterozygote, for it is quite as easy to assume that the movement of the accessory chromosome or "X-element" to the female pole takes place in response to a tension caused by the *absence* of a positive *male* sex-determiner at that pole, as that it is attracted by the *presence* of a positive *female* determiner. If the "X-element" should move into the vacancy caused by the absence of the sex-determiner, the presence of the added chromosome or group of chromosomes would become the evidence of the absence of the sex gene; in other words, the female possessing the added chromosome would be a negative homozygote. All this is highly speculative, and as there appears to be no way as yet to put the matter to experimental test, it seems futile to discuss further the question

whether the female of *Lychnis dioica* is a positive, neutral, or negative homozygote, or whether the synaptic mate of the female gene is qualitatively male or not. The matter has been considered at such length only because it is important that no unwarranted conclusions should be drawn from the configuration of the chromosomes in any given case.

There appears to be no very strong evidence at present that the chromosomes are the representatives or producers of particular Mendelian unit characters, though attempts have been made a number of times during the past decade to identify them as such. On the other hand, there is still no positive and complete demonstration that the chromosomes are *not* the determiners of the Mendelian characters, and until this demonstration is provided, the relation of the chromosomes to the unit characters must be kept open. Whether the chromosomes are responsible directly for sex may well remain likewise an open question for the present, especially in view of the fact that in many animals, and in the few plants which have been thus far investigated, no chromosome differences have been found to differentiate the sexes.

There can be no doubt of course that the sex characters are *associated* with chromosome differences in the considerable number of animals which have been found to present such differences, but, as we have just seen, the nature of this association is not clear. Where two types of sperms are found in the male, the one type corresponding in its chromosome complex with the single type presented by the eggs, the inference is fully justified that such males are heterozygous and the females homozygous in respect to sex, whether one or more chromosomes be the sex-determiner, or whether these chromosomes are merely symptomatic of other fundamental differences which are the true sex-determiners; and vice versa, when two types of eggs having different chromosome groups are found in the female, one of which agrees with the only type found in the sperms, the inference is fair that the female is heterozygous and the male homozygous in respect to sex. So consistent have been the results in those species in which both male and female germ cells have been investigated, that it has not seemed improper to assume that in any given species the one sex will have

uniform germ cells, and is to be considered homozygous, if the other sex is demonstrated to have two types of germ cells.⁶

No chromosome differences have been found in *Lychnis dioica* L. by STRASBURGER (36), who has studied a form of this species known in German taxonomic works as *Melandrium rubrum* Garcke. His careful investigation of germ cells and root tips showed 24 chromosomes to be the somatic number, one pair of these chromosomes being notably larger than the rest, thus resembling the accessory chromosomes or supposed sex chromosomes of the insects. However, in *Lychnis*, the two members of this pair are indistinguishable from each other in both the male and the female. The same results have been independently secured by Miss LUTZ during the past year, but have not yet been published. *Lychnis* appears to agree, therefore, with *Nezara*, *Oncopeltus*, etc. (WILSON 39, 40), among the Hemiptera, as in these the two types of sperms, which doubtless exist, are not visibly differentiated. STRASBURGER (36) reports also that an investigation of *Bryonia dioica* has not revealed the two types of sperms that might *a priori* have been expected.

The hypothesis of unpaired determiners implies that a new Mendelian character originates by the formation of a new gene or the loss of an old one. My interpretation of hermaphroditism in *Lychnis dioica* as due to an alteration in a sex gene already in existence, which alteration does not in any way change the homology of the gene in question, calls for a fundamentally different method of origin of new characters from that involved in this extreme form of the "presence and absence" hypothesis. The new genotype which arises by mutation from the old one has in this case neither more nor fewer genes than had the genotype from which it originated.

The occurrence of male mutants among the offspring of my genetic hermaphrodites appears to me to have a bearing upon this question, as to the mode of origin of new characters. Among the offspring of genetic hermaphrodites tabulated in this paper, 11 male mutants appeared, and under case XII it is shown conclusively that these are true males, and do not again give hermaphrodite offspring, except probably in the extremely small proportion given

⁶ As already noted, GUYER'S (14, 15) studies on spermatogenesis in the domestic fowl and in the guinea fowl appear at present to be exceptions.

by males not derived from a hermaphrodite family. These 11 males appeared in hermaphrodite families comprising a total of 5467 individuals, thus possibly indicating a somewhat greater coefficient of mutability than that reported for the production of hermaphrodites from normal males. It seems therefore that the modification of the gene *M* (or *f*) into a hermaphrodite gene *H*, and the reversal of this modification so that a normal male gene is again produced from a hermaphrodite gene, occurs with somewhat unequal facility, but the difference is not great enough to warrant the belief that mutation in the one direction is caused by the appearance of a new, independent organ, while its reversal is due to the disappearance of that organ. It seems to me more probable that these reversible mutations are due to reversible modifications of an element or organ continuously in existence, and not to the production of a new element or the dropping out of an old one.

The change from a male to a hermaphrodite condition and the reverse are processes both striking and sudden. Perhaps they are as fundamental mutations as those observed among the *Oenotheras*. The interpretation given here of the process of mutation in the sex character of *Lychnis* seems to be available for other mutations as well. The sudden acquirement of new functions by a gene already in existence is different from the conception presented by DE VRIES in *Die Mutationstheorie*, to account for the origin of the *Oenothera* mutants, and is in accord with SPILLMAN's "teleone hypothesis." SPILLMAN (30) is inclined to attribute the remarkable mutations in *Oenothera* to irregularities of mitosis, but in these sex mutants of *Lychnis*, abrupt genotypic modifications have taken place which can hardly be assigned to such irregular mitoses.

One puzzling feature of the inheritance of sex in *Lychnis* is the fact that self-fertilized hermaphrodites produce similar ratios of females and hermaphrodites as are produced when unrelated females are fertilized by sperms from hermaphrodites. Since it is obvious that the two types of offspring are due to the heterozygous character of the male, we are led to the conclusion that even though the hermaphrodite individual is heterozygous in respect to sex, its egg cells⁷ are of a single type like those of the normal female

⁷ Perhaps I should say "its *successful* egg cells."

and carry only the female tendency, while its sperm cells are of two types, one of which has the same sex character as the egg cells, the other bearing the hermaphrodite condition. In my preliminary paper, it was suggested that those eggs may fail to develop which lack the female gene *F*, or which possess the male gene *M*; or that in case the female is a negative homozygote, there might be an extrusion of the male gene during oogenesis. As there are no visible cytological differences between the females and the hermaphrodites, it may not be possible to decide these questions. The relatively small number of seeds in the hermaphrodites, as compared with the females, appears to be favorable to a selective elimination of male-bearing eggs. Another explanation seems possible. A segregation of the female and male genes may conceivably take place earlier than the time at which the germ cells are formed, though it must be admitted that there is little evidence at present that such early segregations regularly⁸ take place in any plant or animal. Such a suggestion has been made by BATESON (2, p. 159), however, in the effort to account for certain interesting instances of coupling. If a segregation of female and hermaphrodite genes could be assumed to take place as early as the formation of a certain primordial cell from which the entire reproductive tissue of the ovary develops, so that the ovules are supplied only with the female genes, the observed uniformity of the egg cells would result. If segregation may take place thus before the spermatocytes are developed, this might also offer an explanation of the exceedingly variable sex ratios which occur in *Lychnis*, for an unequally rapid development of tissues derived from female-bearing cells and male-bearing cells, from the moment of segregation until the spermatocytes are produced, would give an unequal number of female-bearing and male-bearing sperms, and variability in this process would produce irregular ratios. I place no stress upon this hypothesis, however, and am inclined to look for an explanation of the observed phenomena in some sort of selective elimination.

There remains to be considered the relation of the somatic hermaphrodites to the problems of sex determination. The results under cases XIII and XIV show that the hermaphrodite

⁸ They are known to take place occasionally in the production of bud sports.

character of these plants was purely superficial and did not affect the germ cells in any recognizable manner. The only bearing these plants have upon the question of sex determination, I think, is in the evidence they give that genetically normal males may be induced in some unknown way to exhibit female characters. When the male is interpreted as a Mendelian heterozygote in respect to the sex-producing gene, the occurrence of such a somatic modification has the appearance of a simple case of imperfect dominance, such as has been noted not infrequently in other Mendelian heterozygotes. However, the development of male organs (non-functional) in the supposedly homozygous female, when the latter is attacked by the smut (*Ustilago violacea*), gives support to the view held by STRASBURGER (36), that not only the heterozygous sex but both sexes contain in some degree the elements of the opposite sex or the capacity to react in the sexually opposite manner. This fact may perhaps indicate that sex is a more fundamental condition than might be inferred from the frequency with which it behaves as a Mendelian unit character. MORGAN (23) suggests a way in which the appearance of the organs or characters of one sex in individuals of the opposite sex may be explained in harmony with the Mendelian interpretation of sex determination. He assumes that there may be present, underlying the female sex gene, a male element with respect to which all individuals of both sexes are homozygous. This he indicates by introducing *m* into all of his sex formulae. In keeping with common usage among geneticists, he should have used *M*, since he intends to denote the *presence* of maleness.

While recognizing the aptness of this suggestion in removing some of the difficulties in the way of a general application of the Mendelian explanation of sex, I am inclined to the view that the Mendelian nature of sex is of secondary rather than of primary consequence. May not maleness and femaleness be thought of as alternative states, which can be crudely analogized with the acidity and alkalinity of chemical solutions? Just as solutions may be made acid or alkaline in different ways, either by qualitative or by quantitative additions, subtractions, or substitutions, or by a combination of qualitative and quantitative changes, it

is conceivable that the alternative sexual types may be determined in different cases by very different methods, some qualitative, some quantitative, and others both qualitative and quantitative. In some species the sexes appear to represent a much more strongly polarized (?) condition than in other species, and a transition from the characters of the one sex to those of the other is attained only with the greatest rarity, if at all; while in other species the sex conditions may be so nearly balanced or neutral that individuals are not so absolutely determined in their sex relations by their genotypic nature, thus resulting in ever-sporting varieties in respect to sex, such as CORRENS (7) has found in *Plantago lanceolata*.

With such a conception of sex, it also appears probable that sex may be influenced sometimes by external factors as well as by internal ones, and in this case the preponderance of one sex over the other, which has been observed in many animals and plants, need not be attributed alone to a selective disorganization of germ cells, a selective fertilization, or a selective death rate, but might conceivably be controlled to a certain extent by environmental conditions acting at some particular "sensitive period" in the ontogeny of the organism in question. However this may be, there is little or no evidence at present that such environmental influences on sex can be more than relatively slight in the case of dioecious plants and animals. In such organisms recent genetic and cytological studies prove conclusively that sex is generally determined by the genotypic nature of the individual.

Summary

The hermaphrodites of *Lychnis dioica* are modified males. They are of two kinds, which are here distinguished as "genetic" and "somatic" hermaphrodites.

When the genetic hermaphrodites are used as pollen parents, either when self-fertilized or in crosses with females, their progenies consist of females and hermaphrodites. When they are used as pistil parents, and fertilized by normal males, they produce females and normal males.

Somatic hermaphrodites may be externally indistinguishable

from the genetic hermaphrodites, but when used as pollen parents they produce no hermaphrodite offspring, but only females and normal males.

The fact that males can be modified so as to produce functional organs of both sexes, indicates that they are sex heterozygotes, and the production of both females and hermaphrodites by self-fertilized hermaphrodites strongly supports the same interpretation.

The hermaphrodite character can neither find expression in the females, nor can it be transmitted by their eggs to the male offspring. Consequently it is not determined by an independent gene, H , but by a modification of the male sex gene, M , or of the "synaptic mate" of the female gene, F .

If the males and hermaphrodites are heterozygous, it follows that the females are homozygous; but this does not offer an ultimate solution to the relationship between females and males, since there may be several different kinds of homozygotes and heterozygotes. As applied to the relation of the sexes, these may be indicated by the following formulae: (a) The female may be a "positive" homozygote; then $FF = \varphi$, $Ff = \delta$, Ff_H or $FH = \varnothing$. (b) If the female is a "negative" homozygote, $FFmm = \varphi$, $FFMm = \delta$, $FFM_Hm = \varnothing$. (c) When the female is a "neutral" homozygote, $FF = \varphi$, $FM = \delta$, $FM_H = \varnothing$. In each of these formulae the subscript H is intended to represent a modification of the gene to whose symbol it is appended, such that the male is changed to a hermaphrodite. Which of these formulae correctly represents the condition in *Lychnis* can not be determined, but the modified gene which results in hermaphroditism is allelomorphic to F unless the female is a negative homozygote.

Among the offspring of genetic hermaphrodites were a small number of male mutants (11 in 5467), which on breeding proved to be normal males. The occurrence of these male mutants indicates that the modification to the hermaphrodite condition, and back again to the male condition, occurs with but slightly unequal facility, and this circumstance is believed to favor the view that mutation in this case depends upon reversible modifications of some permanent element or organ, rather than upon the origination of a new unit, and its disappearance. This interpretation

bears both upon the nature of mutation and upon the real significance of the "presence and absence" hypothesis.

STRASBURGER has shown that females of *Lychnis dioica* attacked by *Ustilago violacea* become pseudo-hermaphrodites through the production of stamens, which however are non-functional, owing to the fact that the smut produces its spores in the anthers. This seems to justify his conclusion that each sex possesses some of the potentialities of the opposite sex.

The view is expressed that the sexes represent alternative states which in different species may be attained in various ways, through either quantitative or qualitative changes, additions, subtractions, substitutions, or transformations, and that in some instances the action of environment may prove effective in determining which of these states shall find expression. Nearly all the recent investigations indicate, however, that sex is at least predominantly dependent upon the genotypic nature of the individual.

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